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The Growth Rate and Age of Tree Fern Trunks in Relation to Habitats

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Not much is known about the growth rates of trunks and the phenology of leaves in tree ferns. Conant's (1976) ecogeographical studies of some Cyatheaceae were followed by those of Seiler (1981) and Tanner (1983), who investigated leaf turn-over rates and trunk growth in *Alsophila salvinii* and *Cyathea pubescens* respectively. Also, Tryon and Tryon (1982) reported different growth rates and age of some tree fern species. None of the studies, however, correlated growth rates and leaf phenology with habitats. The purpose of the present study was to see if any relationship existed between these growth parameters and habitat.

STUDY AREA

The study area, known as the Reserva Biológica Alberto Brenes, is located on the Atlantic slope of the Cordillera de Tilarán in Costa Rica. The geographical coordinates are 10°12′ N, 84°36′ W. The reserve has an elevation of 850-1150 m. The rainfall is markedly seasonal, with a dry season from the end of December to the middle of April. The mean annual rainfall is 3300 mm (Sprenger 1992). In the life-zone system of Holdrige (1971), this area is classified as premontane wet forest.

METHODS

In March 1991, 233 tree ferns were marked and their height was measured. The species *Alsophila erinacea* (H. Karst.) D.S. Conant (33 plants), *Alsophila polystichoides* (H. Christ) Domin (98 plants), *Cyathea delgadii* Sternb. (37 plants), *Cyathea nigripes* (C. Chr.) Domin (30 plants), *Cyathea pinnula* (H. Christ) Domin (13 plants), and *Cyathea trichiata* (Maxon) Domin (22 plants) were investigated. The trunks had sizes between 20 and 490 cm. Voucher specimens of all species are deposited in the National Herbarium of Costa Rica (CR) and in the Botanischer Garten und Botanisches Museum, in Berlin, Germany (B).

Marked plants were located along a primitive trail system in primary forest and secondary open forest. Between March 1991 and September 1993, we observed the plants and measured their height every 3 to 4 months. We also monitored the number of leaves and the production of sori. Unfortunately all

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TABLE 1. Trunk growth of tree ferns in different habitats in the Reserva Biológica Alberto Brenes, Costa Rica.

	Forest type	Growth (cm/year)
Alsophila erinacea	primary	13.6
Alsophila polystichoides	primary	18.8
Cyathea delgadii	primary	21.3
Cyathea pinnula	primary	10.4
Cyathea nigripes	primary	17.1
Cyathea delgadii	secondary	81.9
Cyathea trichiata	secondary	89.7

the plants of *C. trichiata* and some of *C. delgadii* were destroyed by the construction of a road through the site at the end of February, 1993. For these species, we were able to monitor growth for only 23 months. All other species were monitored the full 30 months.

Statistical analysis of the data on growth and plant size was completed using the standard Wilcoxon paired-sample test at the five percent confidence level (analyses not shown).

RESULTS

The species showed different habitat preferences (Table 1). For example, *A. erinacea, A. polystichoides, C. nigripes* and *C. pinnula* are found only in the primary forest. *Cyathea trichiata* grows only in secondary areas of the forest. Only *C. delgadii* was found both in the primary and in the secondary forest. Although *C. pinnula* grows in primary forest, it mostly occurs in gaps or old open parts. We did not find any individuals of *C. pinnula* more than 2.2 m tall. Within the narrow elevational range (300 m) of the study area, we observed no correlation between elevation and distribution of the species.

TABLE 2.—Summary of trunk growth rates and estimated ages of tree fern species.

	Growth rate (cm/year)	Estimated age of a 5 m trunk	Habitat (forest type)	Source
Cyathea pubescens	6.6	75 years	?	Tanner (1983)
Alsophila bryophila	5.0	100 years	primary	Tryon and Tryon (1982)
Alsophila salvinii	8.3	60 years	?	Seiler (1981)
Cyathea arborea	28.6	18 years	secondary	Conant (1976)
Alsophila erinacea	13.6	37 years	primary	this study
Alsophila polystichoides	18.8	27 years	primary	this study
Cyathea delgadii	21.3	23 years	primary	this study
Cyathea delgadii	81.9	6 years	secondary	this study
Cyathea nigripes	17.1	29 years	primary	this study
Cyathea pinnula	10.4	48 years	primary	this study
Cyathea trichata	89.7	6 years	secondary	this study

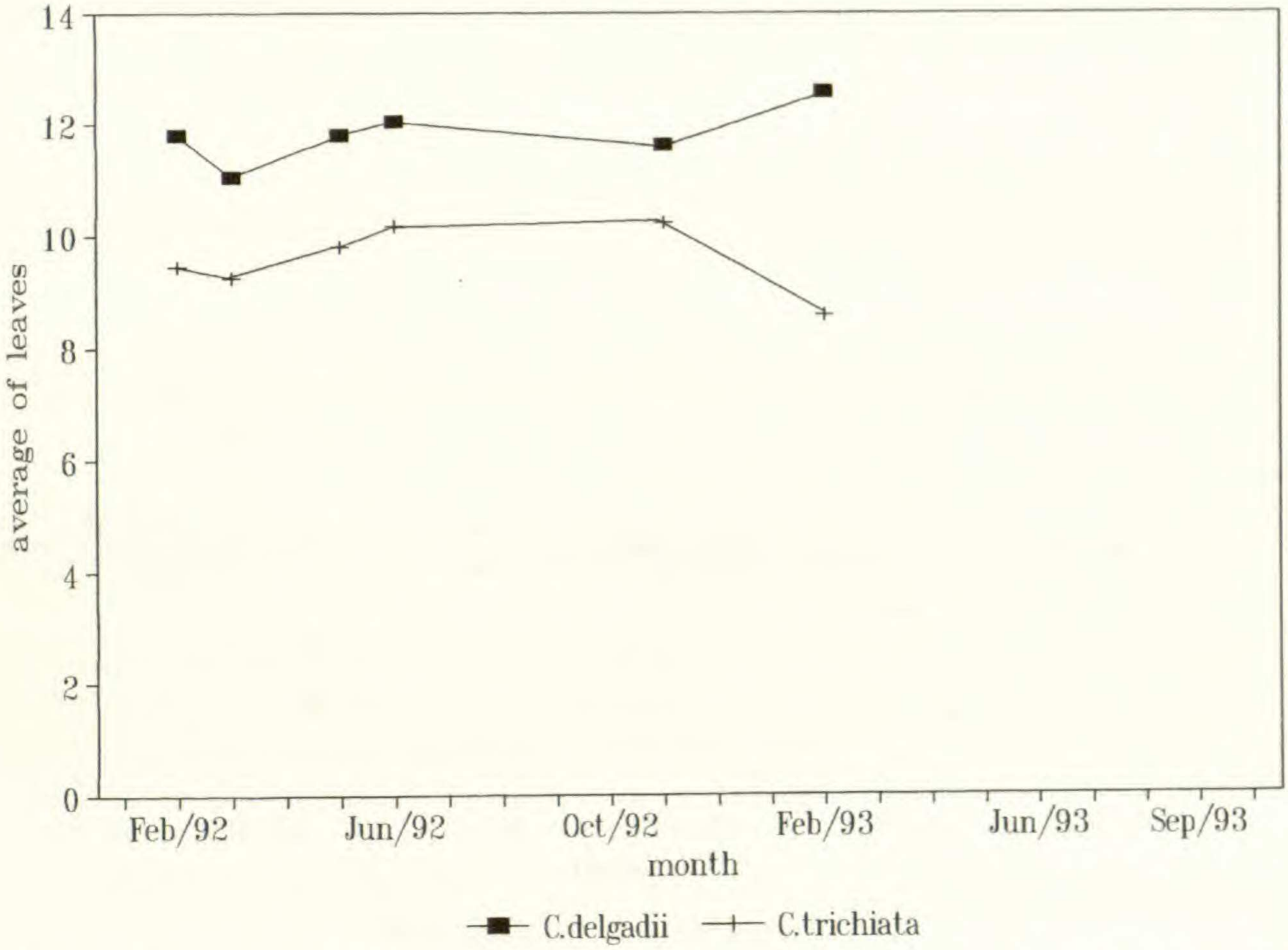

FIG. 1. Average number of leaves from the secondary tree fern species *Cyathea delgadii* (n = 37) and *Cyathea trichiata* (n = 22) from February 1992 to September 1993 (n = number of plants sampled).

The growth rates of the species are various. Over the 23 or 30 month period, the plants grew between 26 and 172 cm (Table 1). Table 1 shows that the two species that occurred in secoundary forest grew three times faster than the species that occurred in primary forest. Statistical tests among the growth rates of individuals from one species point out a confidence level of 95% for all plants with heights between 20 and 490 cm. This result confirms that morphologically different individuals of a species have similar growth rates. On the basis of this information it is possible to evaluate the ages of individuals by their trunk heights, as summarized in Table 2.

The number of leaves per plant is different in the primary and secoundary forest species (Figs. 1–3). The secondary forest species *C. delgadii* and *C. trichiata* showed a high average leaf number over the whole year (Fig. 1). Data for the primary forest species *A. polystichoides* and *C. nigripes* are contrary to this observation. Both species have fewer leaves and lost all of these in April and May (Fig. 2).

Cyathea delgadii (primary), *C. pinnula,* and *A. erinacea* showed a stable number of leaves over the whole year, but fewer leaves than in the secondary forest species (Fig. 3). The production of sori also showed a correlation between species, habitat, and trunk height (age) (Table 3). The secondary forest

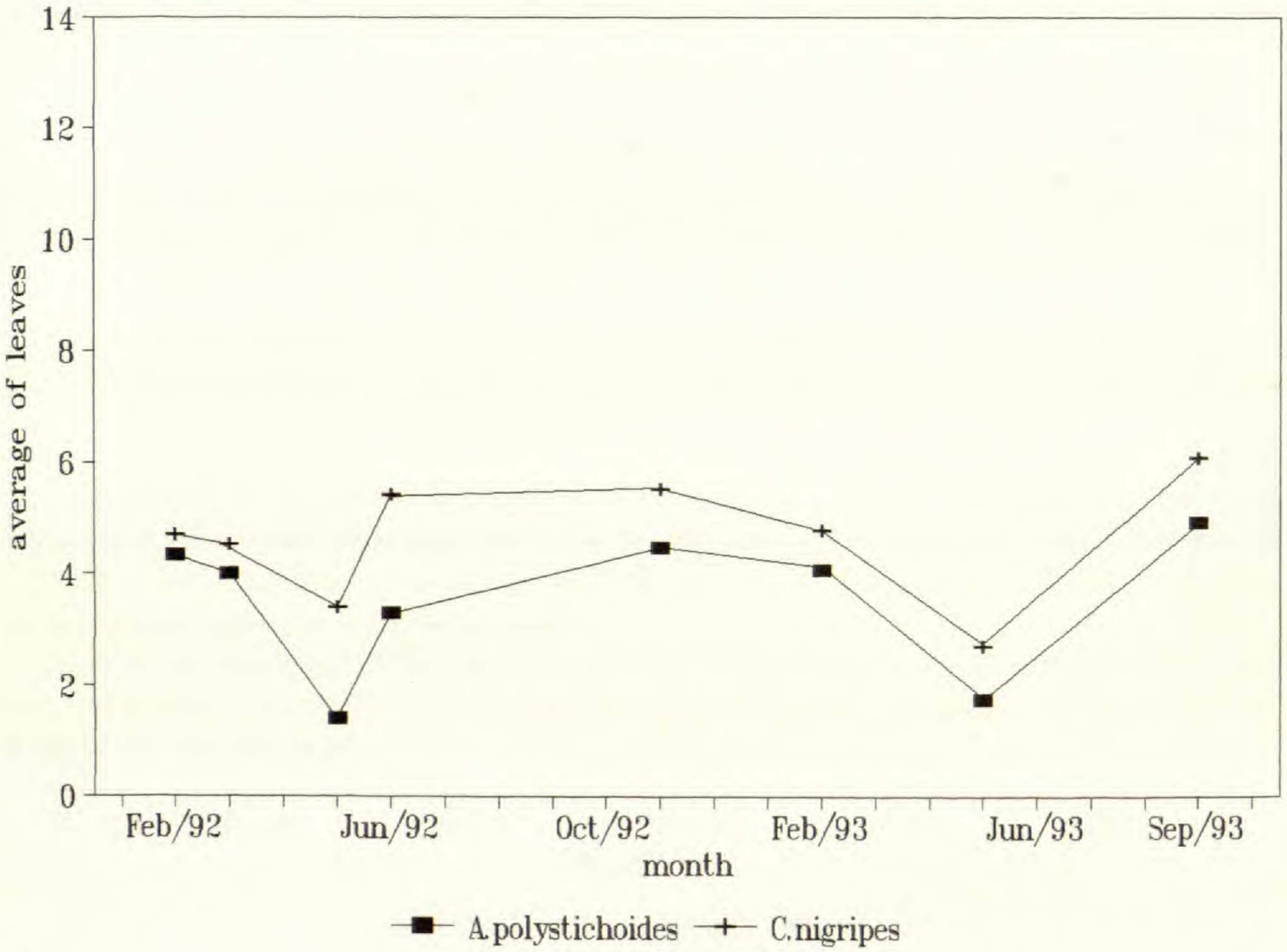

FIG. 2. Average number of leaves from the primary forest tree fern species *Alsophila polystichoides* (n = 98) and *Cyathea nigripes* (n = 30) from February 1992 to September 1993 (n = number of plants sampled).

species showed a very fast development of the sporophyte and the first sori (mostly during the second year). Sori are observed in the primary forest species after about four to six years.

DISCUSSION

The results show that the growth rate of tree fern trunks is influenced by habitat. Those individuals that occur in secondary forest grow three times as fast as in primary forest. This may be true even for individuals of the same species, as shown by *C. delgadii,* which occurs in both primary and secondary forests. These data support similar results found by Conant (1976) concerning the development of the habitat and the forest community. Also, the data of Tryon and Tryon (1982) support the varying growth rates that we detected for different habitats. Important is the rapid growth rate of nearly 90 cm per year by secondary forest species. This is very fast, in comparison with other species (Table 2).

For all calculations of age, a critical problem is that the time required by young sporophytes to develop an erect trunk is not known. After building a

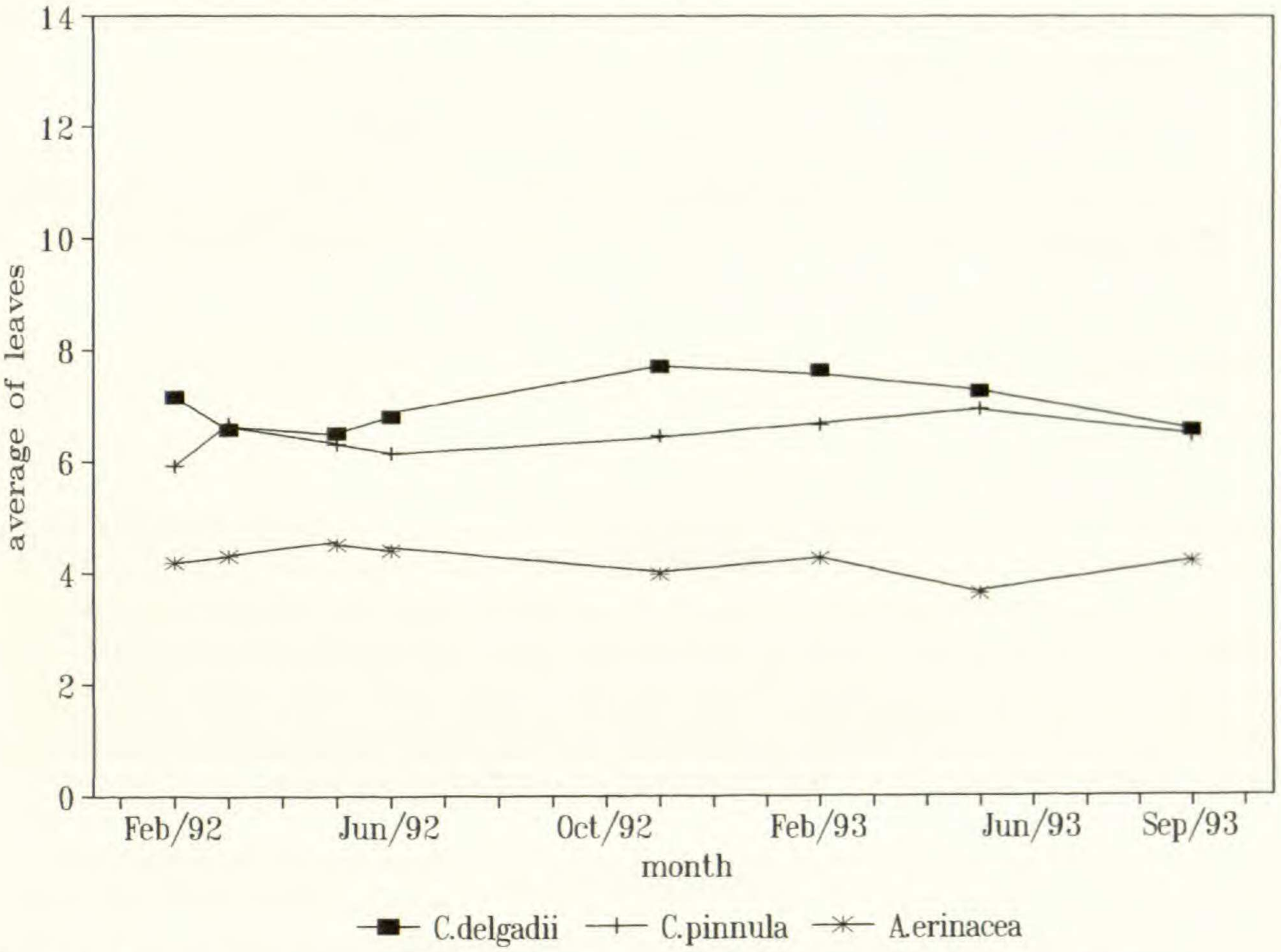

FIG. 3. Average number of leaves from the primary forest tree fern species *Alsophila erinacea* (n = 33), *Cyathea delgadii* (n = 37) and *Cyathea pinnula* (n = 13) from February 1992 to September 1993 (n = number of plants sampled).

trunk, the growth rate is constant. This allows investigators to estimate the age of individual plants.

The differing growth rates of secondary and primary habitat species are a sign of different life-history strategies. Leaf turn-over rates and rapid production of sori in the secondary forest species are arguments for the concept that these are pioneer species. Conant (1976) also suggested this for secondary forest species.

Our data also indicate that different tree fern species live in different habitats. The primary forest plants grow slower and a seasonal turn-over of leaves can be documented (Figs. 1–3). It may be that in the primary forest the plants do not need to grow quickly, because the pressure of competition from other plant species is not as high as it is in the secondary open areas. Also, the increased light allows a for faster growth in the secondary forest.

An exception is *C. pinnula*. This species grows in open parts of the primary forests. The leaf turnover rate and production of sori are typical for a secondary forest species. We believe that it is an example of a fast-growing pioneer in the forests. Later, it is presumably displaced by other tree fern species, which agrees with the plant community concepts of Jacobs (1987).

TABLE 3. Development of sori, in relation to trunk height in tree ferns studied. + = sori observed; 0 = sori lacking; — = no data taken.

	Plant height (cm)							
	0–50	50–75	75–100	100–150	150–200	200–250	250–300	>300
Alsophila erinacea					0	+	+	+
Alsophila polystichoides						0	+	+
Cyathea delgadii (primary)				0	+	+	+	+
Cyathea delgadii (secondary)	0	+	+	+	+	+	+	+
Cyathea nigripes			0	+	+	+	+	+
Cyathea pinnula	+	+	+	+	+	—	—	—
Cyathea trichiata		0	+	+	+	+	+	+

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